

# Principal Components Analysis of Distal Humeral Shape in Pliocene to Recent African Hominids: The Contribution of Geometric Morphometrics

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**ABSTRACT** The shape of the distal humerus in *Homo*, *Pan* (*P. paniscus* and *P. troglodytes*), *Gorilla*, and six australopithecines is compared using a geometric approach (Procrustes superimposition of landmarks). Fourteen landmarks are defined on the humerus in a two-dimensional space. Principal components analysis (PCA) is performed on all superimposed coordinates. I have chosen to discuss the precise place of KNM-KP 271 variously assigned to *Australopithecus anamensis*, *Homo* sp., or *Praeanthropus africanus*, in comparison with a sample of australopithecines. AL 288-1, AL 137-48 (Hadar), STW 431 (Sterkfontein), and TM 1517 (Kromdraai) are commonly attributed to *Australopithecus afarensis* (the two former), *Australopithecus africanus*, and *Paranthropus robustus*, respectively, while the taxonomic place of KNM-ER 739 (*Homo* or *Paranthropus*?) is not yet clearly defined. The analysis does not emphasize a particular affinity between KNM-KP 271 and modern *Homo*, nor with *A. afarensis*, as previously demonstrated (Lague and Jungers [1996] *Am J Phys Anthropol* 111:479–487, 2000).

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In this study, the shape of the distal humeral extremity of large-bodied, modern Hominoidea (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and modern *Homo*) is compared with that of six fossil hominids (AL 288-1, AL 137-48, KNM-KP 271, TM 1517, KNM-ER 739, and STW 431), with a geometric morphometric approach: Procrustes superimposition of landmarks. One principal advantage of this approach is the treatment of shape as a whole by using coordinates of homologous landmarks defined on the contour of the distal humerus. In this respect, the geometry of the bone is preserved, and the variation of its different structural parts (trochlea, capitulum, and epicondyles) can be simultaneously analysed by principal components analysis (PCA) of superimposed coordinates. By taking into account the size parameter (cen-

troid size), australopithecines and modern hominoids can be compared morphometrically, with respect to form and function.

Since the first description by Patterson and Howells (1967), most scientists have agreed that KNM-KP 271 possesses some *Homo*-like features (McHenry and Corruccini, 1975; Day, 1978; Senut, 1979; Leakey et al., 1995, 1998). However, the systematic attribution either to *Homo* sp. (Day, 1978), *Australopithecus anamensis* (Leakey et al., 1995, 1998), or even *Praeanthropus africanus* (Senut, 1995), reflects the real difficulty in determining its closest affinities both

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TABLE 1. List and systematic attribution of fossil hominids

Individuals	Origin	Description and systematic attribution
AL288-1m	Hadar, Ethiopia	<i>Australopithecus afarensis</i> (Johanson et al., 1982)
AL137-48a		
KNM-KP 271	Kanapoi, Kenya	<i>Australopithecus anamensis</i> (Leakey et al., 1995) <i>Homo</i> sp. (Day, 1978; Senut, 1979) <i>Praeanthropus africanus</i> (Senut, 1995)
KNM-ER 739	East Rudolf, Ileret, Kenya	<i>Paranthropus boisei</i> (Leakey, 1971, 1973) or <i>Homo</i>
STW 431	Sterkfontein, Southern Africa	<i>Australopithecus africanus</i>
TM 1517	Kromdraai, Southern Africa	<i>Paranthropus robustus</i> (Straus, 1948)

with modern and fossil hominids. Its provenance, from deposits dated around 4.12–4.17 million years ago in Kanapoi, Kenya (Leakey et al., 1998), raises in particular the question of the direct ancestry of *A. anamensis* to the *Homo* lineage. If some authors are convinced of this phyletic relation to *Homo* (Day, 1978; Senut, 1979; Senut and Tardieu, 1985), others, in support of new discoveries in Kanapoi and Allia Bay, are rather inclined to consider *A. anamensis* as a possible ancestor of *A. afarensis* (Leakey et al., 1995, 1998), while still others do not find any particular morphologic resemblances to modern Hominoids and consider KNM-KP 271 more australopithecine-like (Lague and Jungers, 1996). Because of this ambiguity, my aim was first to determine whether the analysis of the humeral contour in a geometric perspective supports the closer affinity of KNM-KP 271 to *Homo* rather than to apes. Second, I sought to determine the precise phyletic relationship of KNM-KP 271 with other australopithecines, which in this study are represented by five specimens commonly attributed to four different taxa, *Australopithecus afarensis* (AL 288-1m and AL 137-48a), *Australopithecus africanus* (STW 431), *Paranthropus robustus* (TM 1517e), and *Paranthropus boisei* or *Homo* (KNM-ER 739).

Using an exact randomization procedure for the analysis of variation among Plio-Pleistocene hominid distal humeri, Lague and Jungers (1996, p. 402) observed: "Subsequent analyses further support the inference that KNM-ER 739 and KNM-ER 1504 are different from the other hominid humeri and possess a unique total morphometric pattern." This result, suggested before by McHenry and Corruccini (1975), called into question the functional and morphologic

pattern defined by Senut and Tardieu (1985) for the "robust" australopithecine specimens (including TM 1517 and KNM-ER 739, and also KNM-ER 1504 and KNM-ER 3735). In the same paper, the authors further added, "TM 1517 is most similar to one of the Hadar specimens of *A. afarensis* (AL 137-48), whereas the first specimen of *A. africanus* (STW 431) is not closely linked to any of the other australopithecines." Faced with new problems and disagreement, this morphometric analysis is an attempt to assess morphological differences and similarities among the six specimens of fossil hominids, in order to clarify their phylogenetic relationships.

## MATERIALS AND METHODS

### Materials

The sample is comprised of a homogeneous human population studied in the St. Brydes crypt in London ( $n = 73$ ), three species of African apes studied in Tervuren, i.e., *Pan paniscus* ( $n = 20$ ), *Pan troglodytes* ( $n = 22$ ), and *Gorilla gorilla* ( $n = 26$ ), and by the six well-preserved humeri of Plio-Pleistocene hominids, including both casts (AL 288-1m and AL 137-48a from Hadar, KNM-KP 271 from Kanapoi, and KNM-ER 739 from Koobi Fora) and originals (TM 1517 from Kromdraai and STW 431 from Sterkfontein) (Table 1).

### Methods

Photographs of the distal extremity of the humerus in inferior view were taken with the same orientation for all specimens. The humerus is oriented with reference to the biepicondylar line. Following the classification of Bookstein (1991), all landmarks belong to type II (maxima of curvature) and type III (constructed points due to the projection of the contour used).

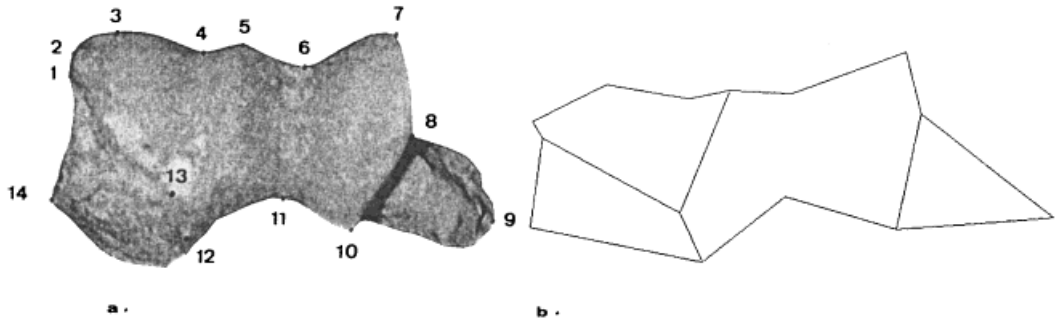


Fig. 1. **a:** Location of the fourteen landmarks on the humeral contour in two dimensions. **b:** Average configuration.

Fourteen landmarks were selected on the contour of the epiphysis in inferior view (Fig. 1): 1) the junction between the lateral epicondyle and the capitulum humeri, 2) the most lateral point of the capitulum humeri, 3) the apex of the capitulum which is the maximum curvature of the capitulum in inferior view, 4) the capitulum groove, 5) the anterolateral margin of the trochlea, 6) the groove of the trochlea in the anterior aspect, 7) the anteromedial margin of the trochlea, 8) the junction between the trochlea and the medial epicondyle, 9) the most salient point of the medial epicondyle, 10) the posteromedial margin of the trochlea, 11) the groove of the trochlea in the posterior aspect, 12) the posterolateral margin of the trochlea (prominence of the lateral trochlear ridge), 13) the junction between the capitulum and the posterolateral margin of the trochlea, and 14) the most salient point of the lateral epicondyle.

Landmarks were digitized using a two-dimensional (2D) digitizing table and the DS-DIGIT program (Slice, 1994a). The centroid size (Bookstein, 1991) was computed as the logarithm of the square root of the sum of squared distances from the centroid to each landmark (Gower, 1975). All raw coordinates were superimposed with the Procrustes method (Gower, 1975; Rohlf and Slice, 1990; Goodall, 1991). A generalized least-squared fit (GLS) was computed using GRF-ND software (Slice, 1994b): an iterative procedure fits the entire sample to an estimated average configuration (dotted-line configurations in Figs. 2, 3). A new av-

erage consensus is estimated at the end of each iteration. Superimposed coordinates were analyzed by principal components analysis (PCA) of the covariance matrix with NTSYS-pc software (1992). Extreme deformations were computed using GRF-ND in order to illustrate the shape variation along each axis of the PCA (solid-line deformations, Figs. 2, 3).

## RESULTS

### PCA of shape differences

The first four axes explain 60.3% of the total variance: 30.4%, 12.8%, 9.6%, and 7.2%, respectively.

The first plot (axis 1/axis 2; Fig. 2) clearly divides three groups with a limited overlap: modern *Homo*, great apes (*Pan*, *Gorilla*), and fossil hominids. The first axis reveals two main humeral shapes: *Homo* on one side, and apes (*Pan*, *Gorilla*) and fossil hominids together on the other side. The variation mainly concerns the proportions of the medial (landmarks 8, 9) and the lateral (landmark 14) epicondyles, the extension of the capitulum in inferior view (landmark 13), and to a lesser degree the depth of the groove of the trochlea humeri (landmarks 6, 11). Compared with the trochlea and the capitulum, the proportions of both epicondyles appear relatively smaller in apes and australopithecines than they are in modern *Homo*. Also, in apes and australopithecines, the position of both epicondyles is also more anterior, relative to the joint surfaces, with the lateral epicondyle salient laterally

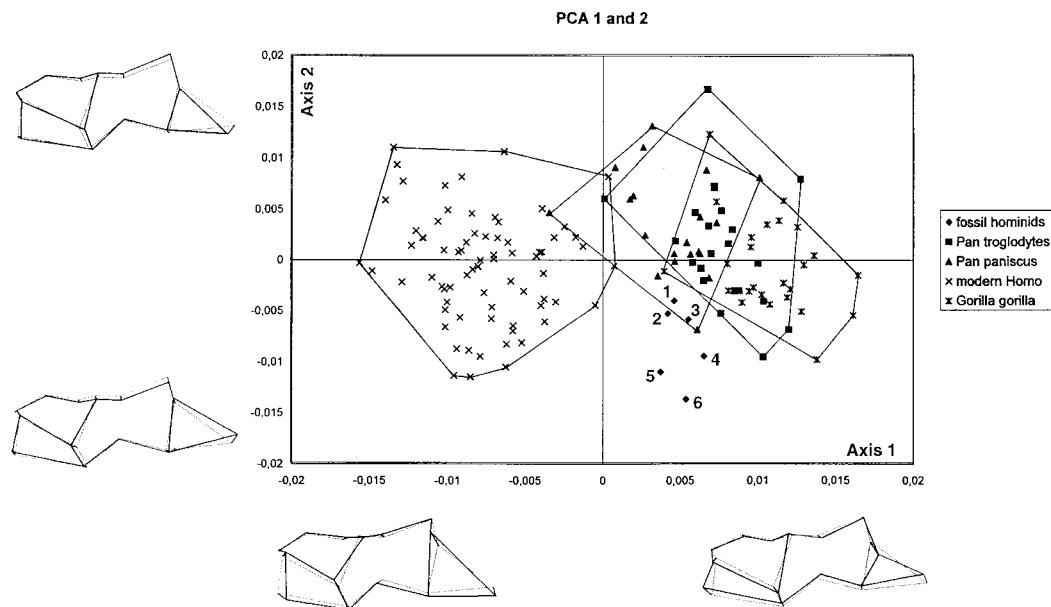


Fig. 2. Principal components analysis of superimposed landmarks for axis 1 (30.4%) and axis 2 (12.8%). Plots of extreme deformations (solid lines) are associated with each axis. Dotted lines correspond to the mean reference configuration. 1, AL 288-1; 2, AL 137-48; 3, TM 1517; 4, STW 431; 5, KNM-KP 271; 6, KNM-ER 739. Convex hulls are depicted for the main taxonomic groups.

(landmark 14); the trochlear groove is deep (landmarks 6, 11); the lateral margin of the trochlea is more "sagittally" oriented (landmarks 5, 13). In *Homo*, we find the opposite characteristics: anteroposteriorly large epicondyles but not salient (especially the lateral one), a shallower trochlear groove, an oblique lateral trochlear margin, and a weak extension of the capitulum.

Concerning axis 2, fossil hominids differ from modern apes. In chimpanzees, the relief of the trochlea in the anterior aspect tends to be better developed than in fossil hominids (landmarks 5–7), and the medial epicondyle appears somewhat posterior (landmark 9) relative to joint surfaces. The posterolateral trochlear crest (landmarks 12, 13) is situated more medially in apes than in fossil hominids, accentuating the width of the trochlea in the latter.

The second plot (axis 3/axis 4; Fig. 3) distinctly reveals three groups among modern apes: *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla*, modern *Homo* and fossil hominids largely overlapping them all. KNM-KP 271 is located outside the variation of the two *Pan* species, but at the mar-

gin of the variation of *Gorilla* and *Homo*. AL 137-48 falls within the variation of *Pan paniscus*, whereas AL 288-1 appears intermediate between ranges of variation of the two *Pan* species. TM 1517, STW 431, and KNM-ER 739 fall grouped within the range of variation of *Pan troglodytes*.

Axis 3 separates gorillas from chimpanzees (*Pan paniscus* and *Pan troglodytes*). This concerns the development and extension in inferior view of the capitulum (landmarks 1–5, 13), in correlation with the depth of the trochlear groove (landmarks 10, 11) and the position of the medial epicondyle (landmark 9). Seen from below, *Gorilla* exhibits a proportionally small capitulum with a mediolaterally large trochlea. Conversely, *Pan paniscus* and *Pan troglodytes* exhibit large, well-developed capitula, and anteroposteriorly massive trochleas.

Axis 4 separates *Pan troglodytes* from *Pan paniscus* only on the basis of the medial projection of the medial epicondyle (landmark 9), which is more marked in the latter.

KNM-ER 739, TM 1517, STW 431, and KNM-KP 271, which share with *Pan troglo-*

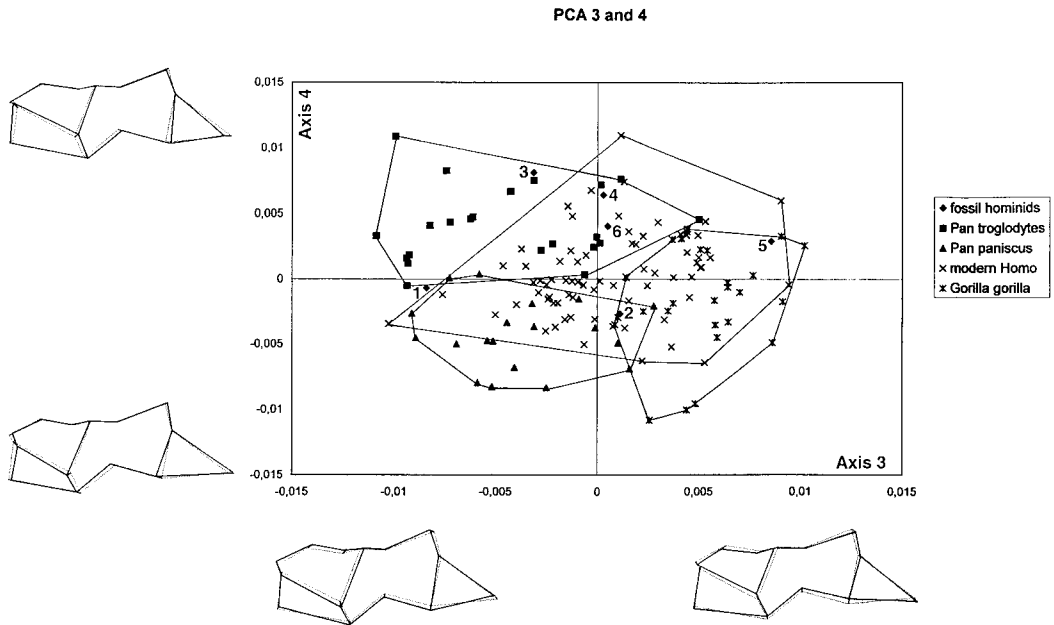


Fig. 3. Principal components analysis of superimposed landmarks for axis 3 (9.6%) and axis 4 (7.2%). Plots of individuals and extreme deformations are associated with each axis. 1, AL 288-1; 2, AL 137-48; 3, TM 1517; 4, STW 431; 5, KNM-KP 271; 6, KNM-ER 739. Convex hulls are depicted for the main taxonomic groups.

*dytes* a medial epicondyle which is not well-developed medially, differ from the Hadar specimens on the basis of this feature.

### DISCUSSION

Morphometric analysis of the distal humeral extremity in a sample of modern hominoids and fossil hominids was undertaken to determine whether KNM-KP 271 is closer to *Homo* than to apes. Also to be determined was whether the morphometric approach could identify the specific phyletic relationships of KNM-KP 271 within the australopithecines.

#### Discrimination among taxa

The first PCA plot undeniably confirms that australopithecines are morphologically homogeneous, especially if we take into account that the degree of overlap in the humeral contour in humans, apes, and australopithecines is minor. This agrees with the data of Hill and Ward (1988), who suggested the difficulties involved in sorting fossil humeri. Lague and Jungers (1996), who used canonical variates analyses of Hominoid hu-

meri (*P. troglodytes*, *G. g. gorilla*, *G. g. beringei*, and Native and African Americans) with a larger fossil sample, previously emphasized the same results. In my analysis, australopithecines are unique among Hominoids, having a particular combination of features, illustrated along axes 1 and 2, such as a medial epicondyle placed more anteriorly relative to the joint surfaces, and a trochlea which is weakly developed anteroposteriorly (Fig. 2).

But globally, taking into account the greater part of variance in axis 1, all australopithecine humeri are closer to those of apes than to those of humans. They share with apes relatively larger articular surfaces (capitulum and trochlea) compared with both epicondyles, and a capitulum markedly extended in inferior view. Apes and australopithecines also share a deep trochlea, a salient lateral anterior trochlear crest, and a salient lateral epicondyle. These features may have a functional meaning in relation to the use of forelimb in arboreal activities, such as suspension or climbing, largely described in the literature



TABLE 2. Size parameters of the humeral epiphysis (logarithm of the centroid size)<sup>1</sup>

Species	Sex	N	x	SD	MIN	MAX
Modern <i>Homo</i>	31 M, 42 F	73	2.682	0.608	2.279	3.264
<i>Pan paniscus</i>	9 M, 9 F	18	2.630	0.205	1.988	3.044
<i>Pan troglodytes</i>	10 M, 3 F	22	2.653	0.286	2.324	3.323
<i>Gorilla gorilla</i>	12 M, 13 F	26	3.908	0.780	3.169	5.090
AL 288-1			2.044			
AL 137-48			2.391			
TM 1517			2.559			
STW 431			2.812			
KNM-KP 271			2.818			
KNM-ER 739			3.253			

<sup>1</sup> M, male; F, female; N, effective; x, mean; SD, standard deviation; MIN, minimum; MAX, maximum.

since the 1980s (Senut, 1981a,b; Stern and Susman, 1983; Susman et al., 1984; Schmid, 1983; Senut and Tardieu, 1985; Coppens and Senut, 1991). The presence of a salient lateral trochlear crest (not so well developed as in *Gorilla* and *Pan* in my analysis) is believed to prevent the dislocation of the joint during arboreal locomotion. The greater extension of the capitulum onto the posterior aspect of the epiphysis could allow a better extension of the elbow. The salience of the lateral epicondyle would suggest powerful extensor muscles of the hand and the digits.

Concerning modern apes, the morphological differences which enable discrimination of the three species are minor (Fig. 3; plots 3 and 4), but it nevertheless appears possible to accurately sort the three taxa of large-bodied apes (*Pan paniscus*, *Pan troglodytes*, and *Gorilla gorilla*) on the basis of the variation of articular elements assessed on plots 3 and 4 (Fig. 3). The results show that part of the shape differences among African apes are size-dependent (Table 3), and that these differences mainly concern the articular surfaces (proportions of the capitulum and the trochlea). Both species of *Pan* present a massive trochlea and a well-developed capitulum. *Gorilla* exhibits a large trochlea with a small capitulum.

#### To what can variation in shape be attributed?

Most shape variations among all australopithecines can be described by an allometric effect, as the large degree of size differences among fossil hominids appears as large as that observed between male and female gorillas. The correlation between co-

ordinates of each fossil on axis 2 and the centroid size ( $r = -0.957$ ,  $P < 0.005$ , Table 3) is the most significant, but only among fossil hominids. These size-dependent features are a flat trochlea with flat anterolateral margins and a medial epicondyle which is more anteriorly projected. These characteristics appear more and more pronounced in AL 288-1, AL 137-48, TM 1517, STW 431, KNM-KP 271, and KNM-ER 739 (Table 2).

According to the distribution of the entire sample (both modern and fossil clusters) into axes 1 and 3 and centroid sizes, it appears evident that the variations between the different groups predominantly describe shape differences. However, a part of these shape differences present an allometric effect. The correlations between shape and size (centroid size) are  $r = 0.488$ ,  $P < 0.05$  for axis 1, and  $r = 0.462$ ,  $P < 0.05$  for axis 3 (Table 3). These size-related features concern first the relative proportions between articular surfaces (trochlea and capitulum) and epicondyles, and secondly, the relative proportions between the trochlea and the capitulum. Concerning this last characteristic (axis 3), the fossils are closer to *Homo*, with a positive allometry, than to *Gorilla* and *Pan*, characterized by a negative allometry.

#### Affinities of KNM-KP 271

With regard to the variation expressed by all specimens, especially as illustrated in the first PCA plot (Fig. 2), the results do not emphasize a particular affinity between KNM-KP 271 and modern *Homo*, as previously assessed by Lague and Jungers (1996). Moreover, it is interesting to note that the features (a relatively large and

TABLE 3. Correlation between size (log of the centroid size) and components of the first four axes of PCA for each modern species and fossil hominids

Species	Axis 1	Axis 2	Axis 3	Axis 4
Fossil hominids (n = 6)	0.314	-0.957**	0.594	0.516
Modern <i>Homo</i> (n = 73)	0.155	-0.192	0.246*	0.022
<i>Pan paniscus</i> (n = 20)	0.355	0.076	-0.330	-0.139
<i>Pan troglodytes</i> (n = 22)	0.057	-0.100	-0.366	-0.150
<i>Gorilla gorilla</i> (n = 26)	0.326	0.111	-0.087	-0.282
All specimens (n = 147)	0.488*	-0.103	0.462*	-0.117

\*  $P < 0.05$ .\*\*  $P < 0.005$ .

gracile trochlea, and a capitulum less extended distally than in the other hominids) on which the *Homo*-like resemblance was based, appear here highly variable in *Homo* as they are significantly related to size (Table 3; correlation between axis 3 and centroid size in *Homo*,  $r = 0.246$ ,  $P < 0.05$ ).

Among fossil hominids, KNM-KP 271 differs also from AL 288-1 along axis 3 by the variation of the contour of the articular elements (capitulum and trochlea) (Fig. 3). In this respect, AL 288-1 clearly presents chimp-like similarities, whereas KNM-KP 271 possesses *Gorilla*-like similarities (the presence of a small capitulum combined with a mediolaterally large and a relatively gracile trochlea). However, these differences are weak and the Kanapoi humerus appears closer to other australopithecines than to any modern group.

#### Differentiation within australopithecines

Axis 4 emphasizes two groups: AL 288-1 and AL 137-48 (Fig. 3, axis 4) appear morphologically distant from all other fossil hominids, but the differences appear to be minor with respect to the ranges of variation of modern Hominoids. The distance observed between the two specimens of Hadar is compatible with intraspecific variation. AL 288-1 and AL 137-48, despite great variation, appear closer to *Pan paniscus* in size (Table 2) and shape (Fig. 3).

In an attempt to differentiate distinct groups within australopithecines, only the plot of axes 3 and 4 (Fig. 3) permits the isolation of KNM-ER 739 and TM 1517, together with STW 431, from the other australopithecines. At the moment, *Australopithecus africanus* presents the closest affinity with the alleged "robust" specimens.

However, taking into account the low amount of variance explained by these axes, the separation of "robust" + *A. africanus* specimens does not appear convincing.

#### CONCLUSIONS

In search of human origins, the literature has often put forward the *Homo*-like affinity of KNM-KP 271 (Patterson and Howells, 1967; Day, 1978; Senut, 1979, 1981a,b; Senut and Tardieu, 1985; Leakey et al., 1995, 1998) in comparison with the other australopithecines, especially *A. afarensis*. On the basis of the morphometric approach of the distal humeral extremity, the results do not show close resemblance between KNM-KP 271 and *Homo*. Some features, however, that have been suggested to reveal human affinities of the Kanapoi humerus are not present in distal view (such as the salience and the position of the lateral epicondyle relative to the capitulum in anterior view, the placement of the greatest anteroposterior diameter of the distal shaft (Patterson and Howells, 1967; Senut and Tardieu, 1985), and the presence of a marked median anterior capsular ligament tubercle (Leakey et al., 1995). In KNM-KP 271, a comparatively mediolaterally large and anteroposteriorly gracile trochlea, and a distally less extended capitulum, were considered to be key features for suggesting a closer resemblance to *Homo* rather than to chimpanzees. However, taking into account here the variation of humeral shape as a whole, no affinity with *Homo* emerges clearly; the analysis particularly shows how large the size-dependent variation of these features is in *Homo*, larger than that seen in apes on most axes. Thus, the resemblance between KNM-KP 271 and *Homo* does not appear

sufficient to support a privileged phyletic relation with this genus.

Concerning systematics, more skeletal material would be necessary to specify the nature of the differences observed between the hominid of Kanapoi and the other australopithecine specimens (i.e., specific or generic?). We do not know the real variability within the different species of *Australopithecus* (aside from *A. afarensis*, we have only one specimen for each species). However, with regard to the homogeneity expressed by the six fossil humeri (plots 1 and 2, Fig. 2), no convincing taxonomic separation can be proposed. The magnitude of differences observed between TM 1517, KNM-ER 739, STW 431, AL 288-1, AL 137-48, and KNM-KP 271 appears as minor as that observed in the unique genus *Homo*. Thus, the results of this study support those of Leakey et al. (1995, 1998), who considered KNM-KP 271 as belonging with other elements discovered in Kanapoi in Kenya to the genus *Australopithecus*, despite the morphologic arguments of Senut (1981b) and Senut and Tardieu (1985). Lague and Jungers (1996) arrived previously at the same conclusions with canonical variates analyses (CVA) of modern and fossil hominoids. The 10 fossil humeri included in their analysis are more similar to each other than they are to any modern group. The main difference is that, in the analysis of these authors, fossils are close to *Pan troglodytes* (axis 1 of the CVA, their p. 418), while in this present analysis (axis 1 of the PCA, Fig. 2), fossils are close to apes (both *Pan* and *Gorilla*).

It must also be emphasized that there is no affinity with *Australopithecus afarensis*, a result which agrees with that previously pointed out by Lague and Jungers (1996). In an attempt to distinguish AL 288-1 from KNM-KP 271, we can only conclude that the former appears to be somewhat more "chimp-like," whereas the second is more "gorilla-like" (axis 3, Fig. 3). Our results show that these shape variations among apes and among the two fossil specimens are highly size-related and do not justify some functional and thus taxonomic distinction.

It can be noted that the features used by Senut and Tardieu (1985) to distinguish KNM-ER 739 in a morphologic and functional subgroup with KNM-ER 1504 and KNM-ER 3735 (i.e., the presence of an articular surface not very much different from the modern human one; that of a lateral trochlear crest poorly salient and a lateral epicondyle which is strongly laterally salient) do not appear to be as pertinent in this morphometric approach, as they are highly related to size parameters among all australopithecines (axis 2; Fig. 2), especially the two latter features. Neither "human-like" nor "ape-like" affinities can be accurately extracted for KNM-ER 739 and TM 1517. These specimens cannot be separated from any other fossils, both in size and morphometric profile.

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